Zusammenfassung

Soziale Umwelt junger Gemsen (Rupicapra pyrenaica p.) aus den Pyrenäen während der Ontogenese

Die soziale Umwelt junger Gemsen *(Rupicapra pyrenaica p.)* aus den Pyrenäen wurde einige Monate lang untersucht, um die Entwicklung partieller sozialer Prozesse zu verfolgen. Wir nehmen an, daß das Sozialverhalten der Adulten zum großen Teil durch die Ontogenese bestimmt wird. Von 2001 Gruppen in offenen Bergregionen werden Alters- und Geschlechterverteilung beschrieben.

Während der Kindheit durchlaufen Gemsen beim Kontakt mit Artgenossen allgemein und innerhalb von Weibchengruppen im besonderen soziale Perioden. Beide Muster der Verbände können eine Rolle im Sozialisierungsprozeß spielen. Kitz-Bock-Kontakte erfolgen erstmals in der Brunstzeit und sind seltener. Die drastischsten Veränderungen in der sozialen Umwelt erfolgen in der nächsten Geburtsperiode. Im Frühjahr findet eine besonders sensible Sozialisierungsperiode statt, in der soziale Vereinigungen sehr wechselhaft sind und neue soziale Netzwerke entstehen. Die Rolle der Erfahrung der Ontogenese bei der Bildung sozialer Verbände wird diskutiert.

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Capture-recapture study of a population of the Mediterranean Pine vole (*Microtus duodecimcostatus*) in Southern France

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Abstract

Investigated the population dynamics of a *Microtus duodecimcostatus* population by capture-recapture in Southern France during two years. The study was carried out in an apple orchard every three months on a 1 ha area. Numbers varied between 100 and 400 (minimum in summer). Reproduction occurred over the year and was lowest in winter. Renewal of the population occurred mainly in autumn. The population contained erratic individuals which did not take part in the reproduction. Resident individuals had a longer life-span and home ranges always located at the same place. Mean adult body weight varied only among females in relation to the reproductive rate. The observed demography of *M. duodecimcostatus* could be explained by biological traits (litter size, longevity) and by features of the habitat (high and constant level of resources, low level of disturbance), suggesting that social behaviours are an important regulating factor of numbers.

Introduction

The Mediterranean pine vole (*Microtus duodecimcostatus* de Sélys-Longchamps) has a narrow geographic range: Portugal, Spain and Southern France (Niethammer 1982). Its population dynamics in natural habitats is unknown. The Mediterranean pine vole lives also in cultivated areas. Vineyards are very ancient in the Mediterranean Region (several centuries), and the Mediterranean pine vole is abundant in such a habitat though it causes no particular damage. But the culture of perennial plants (e.g. orchards) with summer irrigation transformed the Mediterranean pine vole's habitat in such a way that this rodent species has become a pest to agriculture for a few years (Guédon 1987, 1988). This indicates the potentialities of *Microtus duodecimcostatus* to colonize successfully particular habitats.

A research program conducted by several institutes (Association de Coordination Technique Agricole, Institut de la Recherche Agronomique, Service de la Protection des Végétaux) was started in 1986. The aim of this program is to study reproductive biology and population ecology of the Mediterranean pine vole and to develop an integrated struggle system (a risk foresight method and biological, chemical, physical, mechanical, and agricultural struggle methods based on a good knowledge of the species). We here present demographic data from a study focused on local population dynamics of *Microtus duodecimcostatus* in cultivated areas.

Material and methods

A capture-recapture study was started in 1989 in Southern France, in an arcea located 30 km east of Montpellier (43° 39′ N, 4° 11′ E). The region is an agroecosystem with intensive cultures distributed in many patches separated by thick boundaries made with shrubs, cypress or poplar. During two years we trapped a population in a 20-year-old apple orchard (Golden Delicious/E.M.9; pollinization is

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made by branches of other varieties). The main agricultural practices are: cutting and crunching of the branches in winter, regular weeding, chemical treatment by pulverization all along the cultural cycle, chemical manuring. The influence of the Mediterranean climate is partially masked because of summer watering. The main disturbance which occurred during the study was a plough partially breaking up the soil in winter 1989. No chemical treatment against the Mediterranean pine vole was carried out during our study. Presence of this vole is revealed, as this species digs up soil from the ground when it is burrowing.

The trapping procedure for subterranean rodents was developed by Pascal (1984; Pascal and Meylan 1986) for the fossorial form of the water vole (*Arvicola terrestris scherman*). This procedure was adapted for snap-trapping (Guédon and Pascal 1992) and for live-trapping of the Mediterranean pine vole (present study). We used Longworth traps (baited with apple) the efficiency of which has previously been demonstrated (Guédon et al. 1990). Traps were distributed on a 1 ha area, along six parallel 5 m × 100 m strips divided into 25 m^2 squares (Fig. 1). Two trap-stations (when possible) were

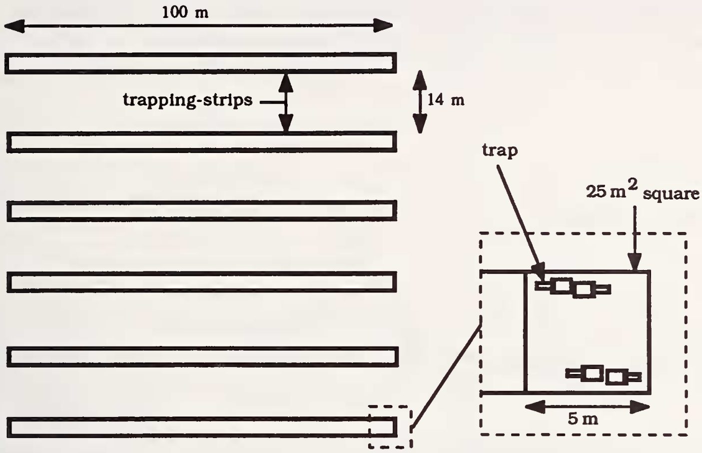

Fig. 1. Arrangement of the traps in the study area. In each square two, one, or no trap-station(s) were arranged in relation to the number of presence signs of Mediterranean pine vole on the ground. Each trap-station contained one, two or three traps

arranged in each square, each trap-station contained one, two or three traps orientated in the axis of the tunnel previously dug out. Each trap was open during 42 hours, and was checked 7 times. The caught animals were weighed (to the nearest g), marked by toe-clipping and ear-cutting, reproductive conditions (males: testes scrotal or abdominal, females: pregnant, lactating, and vulva open or closed) and coat color were noted before being released. It was also noted whether the trap was covered up with soil by the vole (named "trap-stuffing" by Krebs and Boonstra 1984), which is a typical behaviour of this species when its tunnels are opened. Two age-classes were distinguished according to weight, adult: > 17 g, and juvenile: ≤ 17 g. Strips were trapped two by two, so a trapping-session lasted 9 days. Trapping-sessions were carried out every 3 months.

Results

Demography

We caught 1,534 animals 4,656 times in 18,818 trap-checks. The observed numbers (Fig. 2) varied according to the seasons, with a decrease during summer droughts. Proportion of juveniles in the population was always low (Fig. 2). Sex ratio of the caught animals never differed from 1 : 1 (χ^2-tests), for adults as well as juveniles (Fig. 3, the greater fluctuations observed among the juveniles are caused by their smaller numbers compared with the adults).

Among the 429 individuals caught in February 1989, five were recaught in February 1991 (3 males and 2 females of which one was pregnant).

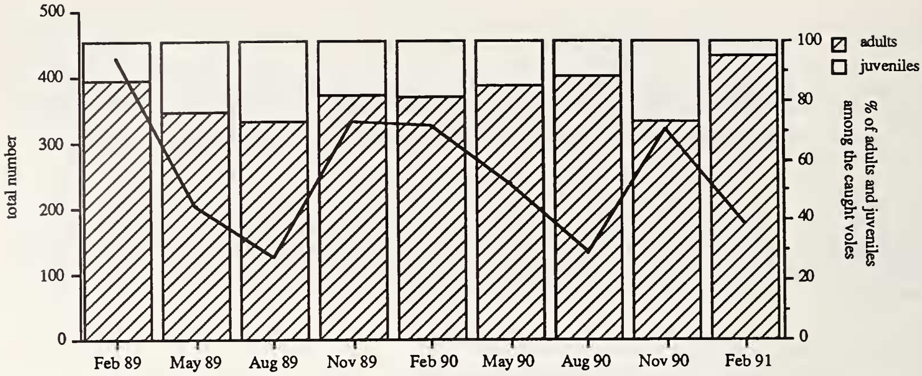

Fig. 2. Total number of caught voles (curve) and percentage of the two age-classes (histogram) during two years

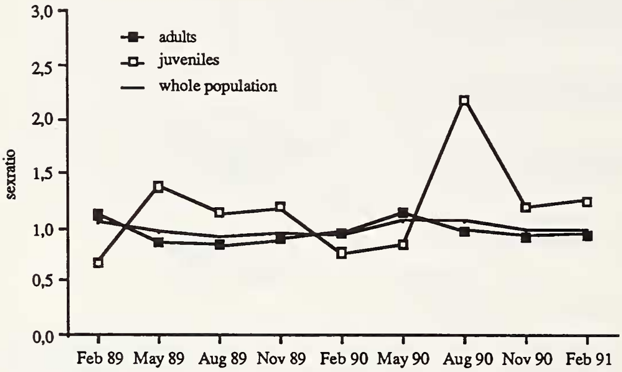

Fig. 3. Sex ratio of the juveniles (voles less than 18 g), the adults (voles heavier than 17 g), and all the voles caught (juveniles and adults)

Reproductive activity occurred over the year but showed seasonal variations. We exceptionally observed male individuals with scrotal testes, indicating that this position of testes is not a reliable sign for sexual activity in male *M. duodecimcostatus.* The proportion of females sexually active was at maximum in May, August and November, but seemed to show inter-annual variations (Fig. 4). This is corroborated by the proportion of juveniles

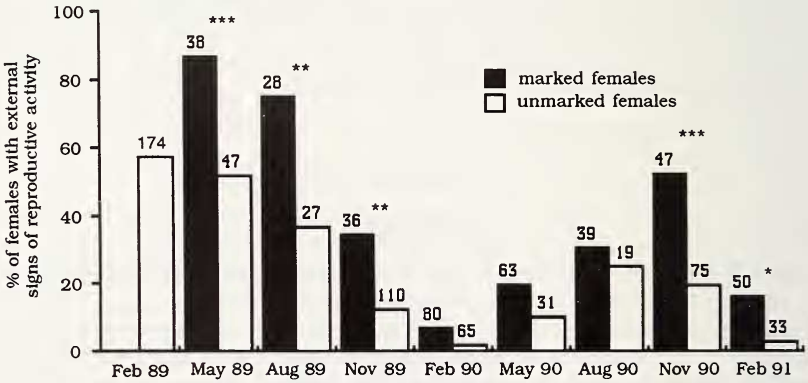

Fig. 4. The adult females caught during each trapping-session are divided into two categories: marked and unmarked (numbers of each category caught are indicated). The proportion of individuals with external signs of sexual activity for each category are plotted and compared (χ^2-tests, *0.01 < p < 0.05; **0.001 < p < 0.01; ***p < 0.001)

Table 1. **Mean body weight of the caught voles in each trapping-session**
(mean ± standard deviation)

session		Feb 89	May 89	Aug 89	Nov 89	Feb 90	May 90	Aug 90	Nov 90	Feb 91
adults	males	22.1 ± 2.2	21.8 ± 1.8	21.1 ± 1.9	21.1 ± 1.8	21.1 ± 1.7	20.7 ± 1.7	21.5 ± 1.7	21.0 ± 1.9	20.6 ± 1.4
	females	23.0 ± 2.8	23.3 ± 3.0	23.6 ± 1.8	22.4 ± 2.4	21.5 ± 2.1	22.0 ± 2.8	24.2 ± 1.6	21.8 ± 2.2	21.4 ± 2.3
juveniles	males	14.9 ± 2.2	14.9 ± 2.0	15.2 ± 2.1	13.4 ± 2.0	15.0 ± 2.0	14.8 ± 2.0	13.3 ± 2.3	14.4 ± 2.0	17.0 ± 0.0
	females	14.9 ± 2.3	14.2 ± 2.2	14.1 ± 2.4	15.3 ± 1.6	14.4 ± 2.3	14.4 ± 2.4	13.8 ± 1.9	14.7 ± 2.3	15.5 ± 2.6

in the population: maximum in August 1989 and in November the following year (Fig. 3). Captures of pregnant females which were lactating confirmed the existence of post-partum fecondation as was observed in the laboratory (Guédon et al. 1991a). The distinction between marked adult females (present for at least 3 months) and unmarked ones shows the following pattern: the proportion of females with external signs of reproductive activity was always higher among the former than among the latter (Fig. 4). This difference is not always statistically significant (χ^2-tests).

The variations in mean body weight of the caught voles did not show seasonality (Tab. 1). Mean adult body weight was slightly higher for females in contrast to males (range: 21.5–24.2, and 20.7–22.1, respectively), due to the presence of pregnant females. Standard deviation of adult body weight was slightly larger for females than for males (range: 1.6–3.0, and 1.4–2.2, respectively); this is probably due to the heterogeneity of pregnancy among the females (Fig. 4).

The proportion of unmarked animals (immigrants, animals born during the three previous months, or residents not previously caught: Fig. 5) varied with the seasons: it was at minimum in August and at maximum in November, indicating that renewal of the population occurred mainly in autumn.

Individual movements recorded during the study

Despite the low distance between two trapping-strips (20 m), the recapture rates from one strip to another were very low (0.4–16 %) indicating that, either movements of the Mediterranean pine vole were very restricted during the time of a trapping-session, or a decrease in the trappability of the voles occurred after a first capture. Analysis of movements between two trapping-sessions corroborates the former explanation: the majority of animals was recaught at the same place as they were caught three months before. Such sedentary animals were observed during several consecutive sessions: among 48 animals caught in four consecutive sessions, 38 (79 %) were always located at the same place. Home range locations seem constant over time, however, we cannot speculate on variations of home range sizes.

The proportion of animals caught twice or several times during the 7 checks (within trapping-session recapture rate) varied with the seasons (Fig. 6), suggesting a decrease in trappability during summer. This proportion was always higher for marked than unmarked animals (except August 1989).

Parameters related to the trapping procedure

Trapping-intensity varied slightly with the seasons: at minimum in August, and at maximum in November (Fig. 7). These variations were related to the lesser number of presence signs on the ground. Proportions of captures and of trap-

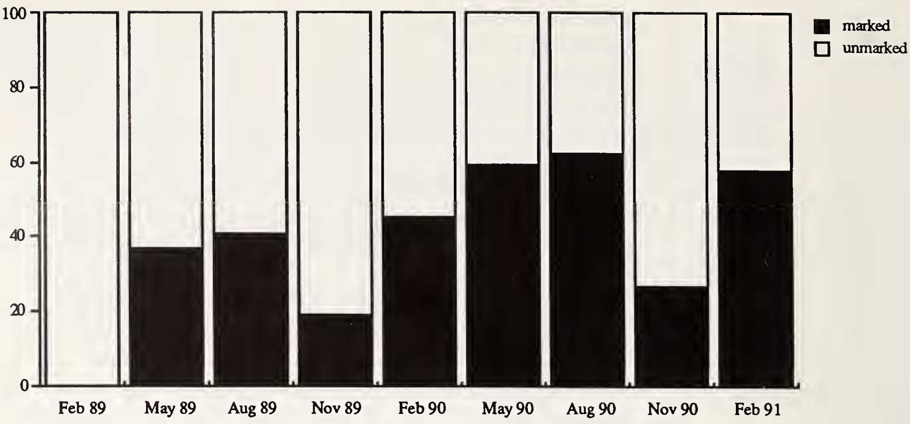

Fig. 5. Proportions of marked and unmarked voles caught in each trapping-session

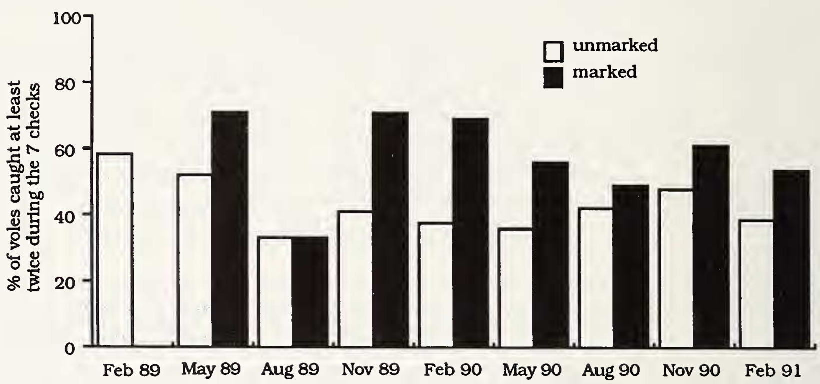

Fig. 6. Comparison of the proportion of voles caught at least twice during the 7 checks (within trapping-session recapture rate) between marked and unmarked voles

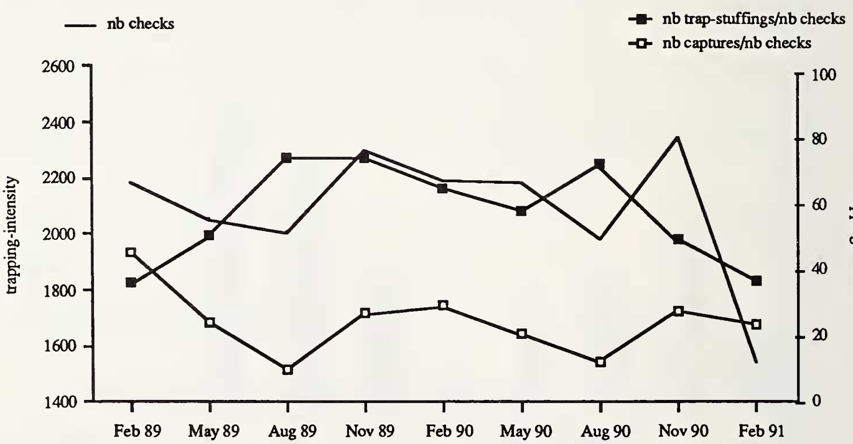

Fig. 7. Trapping-intensity (expressed as number of trap-checks: left axis) and trapping-results (number of captures and number of trap-stuffings reported to the number of checks: right axis) in each trapping-session

stuffings (reported on trapping-intensity) varied greatly with the seasons (Fig. 7). The proportion of captures was at minimum in August (= 10 %) and varied between 20 % and 45 % for the other sessions, the results of February 1989 (45 %) were not obtained again in 1990 and 1991. The proportion of trap-stuffings varied inversely with the proportion of captures.

Other species

Five other species were caught in our traps: *Crocidura russula, Apodemus sylvaticus, Mus musculus, Rattus norvegicus,* and *Mustela nivalis*. Numbers of captures for these species are indicated in Table 2. Herbivorous and granivorous small mammals were scarce in the underground habitat suggesting that competitive interactions with *M. duodecimcostatus* are

Table 2. **Numbers of captures for other species in the Longworth traps disposed in the underground habitat of *M. duodecimcostatus***

species	Feb 89	May 89	Aug 89	Nov 89	Feb 90	May 90	Aug 90	Nov 90	Feb 91
Crocidura russula								1	
Apodemus sylvaticus	8	6	2	1	2			2	1
Mus musculus								1	
Rattus norvegicus					1				
Mustela nivalis			1						

not important in our study area. Only one weasel (*Mustela nivalis*) was caught, indicating that predation by this species may not influence the population dynamics of the Mediterranean pine vole in our study area. A domestic cat (*Felis catus*) was observed in the orchard while hunting; however, raptor birds (*Strix aluco, Buteo buteo, Falco tinnunculus*) were regularly observed and were probably the main predators of the voles.

Discussion

Nearctic and Palearctic pine vole species are generally all included in the "*Pitymys* group" which is considered as a genus (Honacki et al. 1982; Corbet and Hill 1991) or as a subgenus included in the genus *Microtus* (Niethammer and Krapp 1982; Nowak and Paradiso 1983). Chaline et al. (1988) argued that the subgenus *Pitymys* is polyphyletic and proposed to divide it into the two subgenera; *Pitymys* (nearctic species) and *Terricola* (palearctic species). If Chaline et al. (1988) are right, it would implicate a converging evolution of some characters (particularly life-history traits as will be shown below) between *Pitymys* and *Terricola*.

In our population of *M. duodecimcostatus* we observed a decreased trappability during summer. The same phenomenon was observed in *M. pinetorum* (Lindquist et al. 1981; Cornbower and Kirkland 1983) and several *Microtus* species (Krebs and Boonstra 1984). Added to the fact that the proportion of trap-stuffings increased in summer, this leads us to invoke a more subterranean behaviour of the Mediterranean pine vole in order to avoid the hot and dry atmosphere. This changing behaviour may explain the decrease in captured voles during summer, however we cannot exclude a mortality peak during this season.

The age-classes chosen in our study were *ad hoc*: animals less than 18 g weighed more than 17 g three months later. A snap-trapping study demonstrated that some females less than 18 g could already be pregnant (Guédon unpubl. data). Body growth may be slower in nature than in captivity (Guédon et al. 1991b). However, the proportions of juveniles were always low. This can be explained by a low trappability of this age-class: voles were not caught before they weigh at least 8 g. Mc Guire and Novak (1984) and Salvioni (1988) observed that behavioural development was slow in juveniles of other pine vole species (*M. pinetorum* and *M. subterraneus,* respectively). Several studies showed that the proportion of juveniles was always low in populations of *M. pinetorum* (Simpson et al. 1979; Lindquist et al. 1981; Cornbower and Kirkland 1983). Fecundity in pine vole species is low compared with other *Microtus* species or other microtine genera (Lefèvre 1966; Pelikán 1973; Schadler and Butterstein 1979; Salvioni 1986; Guédon et al. 1991a, see Innes 1978 or Keller 1985 for reviews), and may influence the age-structure of the population.

A long life-span was observed in other pine vole species (Le Louarn 1974; Cornbower and Kirkland 1983; Salvioni 1986), and seems to be a trait of these microtine species. Some studies suggested that populations of *M. pinetorum* present a high turn-over (Miller and Getz 1969; Staples and Terman 1977; Simpson et al. 1979). Such a pattern is also present in our study; however, preliminar statistical analysis revealed that this was an artifact: most of the unmarked individuals were erratics and were not subsequently recaught (Paradis 1990).

The fact that reproduction occurs over the year in *M. duodecimcostatus* was also observed in Spain (Claramunt 1976; Palomo et al. 1989), and in populations of *M. pinetorum* living in orchards (Simpson et al. 1979; Cornbower and Kirkland 1983), though this species lives in a cooler climate. Reproduction in our population was at minimum during winter. This result is not in agreement with Palomo et al.'s study (1989) who showed that reproduction decreased dramatically during summer. This result is supported by a small number of caught animals (210 individuals during 2 years and only 4 females in summer), however, and a monthly snap-trapping study in Southern France (more than 7,000 individuals caught during 5 years) showed that reproduction decreased in June and July but increased in August (Guédon and Pascal unpubl. data). Discrepancy in the results of the two approaches (snap-trapping and live-trapping) can be explained by the fact that pregnancy cannot be detected in alive voles before about 10 days, but it can be determined at a state of about 6 days in dead samples (Keller 1985). Cohen-Shlagman et al. (1984) observed a decreased reproductive activiy in summer in *Microtus guentheri,* another Mediterranean microtine species. The seasonal variations of reproduction observed in our population could be explained by high summer survival of resident individuals due to high level of resources in underground habitat of apple orchards. This hypothesis could be tested by studying seasonal variations of reproduction in uncultivated habitats.

In the studied habitat, food is abundant and uniformly distributed, therefore reproduction is probably conditioned by available space (possibility to construct a burrow). In a population with sustained high densities, space is probably a limiting factor for access to reproduction (at least for females). This assumption is strengthened by the fact that reproductive females are resident (present for at least three months). Social behaviours were evidenced to mediate access to reproduction in many species of mammals (Hendrichs 1983; Dunbar 1985; Armitage 1987). Such a phenomenon may play a role in the local population dynamics of *M. duodecimcostatus.*

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